



Large changes in carbon storage under different land-use regimes in subtropical seasonally dry forests of southern South America



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ABSTRACT

Net emissions of CO₂ from land-use conversion represent a significant driver of global climatic change. This is especially true for subtropical seasonally dry Chaco forests from southern South America, now experiencing one of the highest loss rates globally. However, direct quantifications of the effect of accelerated deforestation on carbon (C) pools of these systems are rare. Considering five dominant ecosystem types within the dry Chaco forest of Argentina, derived by land-use change from the same original vegetation, substrate, and climate, we quantified the magnitude and change of total C pools including trees and shrubs, non-woody plants, coarse and fine debris, and soil organic (SOC) and inorganic (SIC) pools up to 2 m depth. Soil C pools represented the largest C stocks (>74%). Shrubs also represented a large C pool (at least 28% of the aboveground standing biomass), which we quantified in detail for the first time. The conversion of forests to open shrublands and croplands was associated to large losses of organic C both in aboveground biomass and in soils down to 30 cm depth (from 43 to 64%). Although SIC is usually considered as a relatively stable compartment, the forest to crop transition presented here involved carbonate losses of c. 68% at soil depths between 1 and 2 m. Our results indicate that the landscape transformations expected in the region under business-as-usual socioeconomic scenarios will probably lead to a marked reduction of the C stored, with a consequent net C emission and a decline in other C storage-related ecosystem services provided by these ecosystems.

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1. Introduction

Unequivocal evidence of global climatic change as a result of rising levels of CO₂ in the atmosphere (IPCC, 2013) has stimulated interest in the conservation and enhancement of natural biological reservoirs of carbon (C), particularly forests. Land-use changes, including forest cover replacement by crops and grazing lands, are one of the main proximate causes of the average annual net CO₂ emissions of 0.9 Gt of C to the atmosphere in the last decades (IPCC, 2013; Peters et al., 2013; van der Werf et al., 2009).

In spite of having one of the highest rates of annual cover loss globally (Hansen et al., 2013), the subtropical seasonally dry forests of southern South America have been comparatively less studied than temperate and tropical forests, where the effect of land-use

on the carbon pools and associated emissions are fairly well studied (Baccini et al., 2012; Don et al., 2011; Harris et al., 2012; Saatchi et al., 2011). The Chaco forest – the geographically most extended seasonally dry forest in South America – is now undergoing massive clearing for agricultural expansion, including annual crops and to a lesser extent grazing lands. In particular, the annual deforestation rates reached by the Chaco forests of Argentina during the last decade are among the highest in the world (Hansen et al., 2013). Emissions from deforestation in the semi-arid Chaco forests of the same region between 1996 and 2005 have been estimated at 15.65 GgC y⁻¹, representing the largest source from land-cover change in the subtropical forests of southern South America (Gasparri et al., 2008).

The process of C loss from vegetation removal due to forest management and deforestation is often accompanied by direct C losses from surface soils as a result of a reduction in its physical protection and a rise in soil temperature in the short term (Martínez-Mena et al., 2002; Post and Kwon, 2000), as well as a reduction in the amount of litter fall in the long term (Don et al.,

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2011; Jandl et al., 2007; Yanai et al., 2003). In the Chaco forest, previous works have found a significant decline in soil organic C (SOC) from the top 0–20 cm (ranging from 33 to 78% of C loss) due to overgrazing and forest degradation (Abril and Bucher, 2001; Bonino, 2006). Deeper soil is assumed to be largely insensitive to the effects of management activities (Dungait et al., 2012; Jandl et al., 2007). However, land-use practices could re-distribute SOC within the soil profile (e.g., by tillage) leading to a priming effect (i.e., a stimulation of C mineralization in deeper layers due to the supply of fresh plant-derived C from surface layers) (Chaopricha and Marín-Spiotta, 2014; Fontaine et al., 2007); or simply by breaking the soil structure and making C more available to decomposers (Salomé et al., 2010; Schmidt et al., 2011). There is also increasing evidence that root-derived inputs drive SOC storage and stability along the soil profile in different ecosystems (Kätterer et al., 2011; Rasse et al., 2005; Tefs and Gleixner, 2012). Since dominant woody species from water-limited ecosystems are expected to have deep root distributions (Schenk and Jackson, 2005; Schenk, 2005) and high allocation to belowground biomass (Poorter et al., 2012), a change in the vegetation cover (e.g., the replacement of forest by non-woody vegetation or crops) could affect SOC vertical distribution and reduce the amount of belowground carbon input, especially in deeper layers (Jobbagy and Jackson, 2000). To date, there is no published empirical record of the SOC compartment below 30 cm for the Chaco forest, or its response to land-use change.

Generally the quantification of soil C has been focused on the organic compartment (SOC) because it is more ubiquitous, while soil inorganic C (SIC, primarily as calcium carbonate) is generally restricted to arid and semi-arid regions, and becomes more important with soil depth (Lal and Kimble, 2000; Schlesinger, 1982). In addition, SIC has been considered to be much less sensitive to land-use changes than SOC (Sanderman, 2012). However, irrigation, the use of fertilizers and other land management practices that alter soil CO₂ levels, pH and dissolved salt concentration, could enhance either carbonate precipitation or its dissolution, thus changing the size of the SIC pool (Lal, 2004; Mi et al., 2008; Wu et al., 2009). Recent studies in semi-arid woody ecosystems of central Argentina have shown that forest disturbance produce significant changes in the water content and salinity of soils (Jayawickreme et al., 2011; Marchesini et al., 2013), which could have significant consequences for the C dynamics of a long-term reservoir like SIC. Although SIC can be the main form of C in the dry and deep soils of semi-arid ecosystems (Sanderman, 2012) like Chaco, to our knowledge no empirical work quantifying this pool have been carried out in this ecosystems.

Methods for C estimation are well established and standardized for tropical and temperate forest across the world (Brown, 1997; Chave et al., 2014, 2005; Don et al., 2011; Gibbs et al., 2007; Keith et al., 2009; Marín-Spiotta and Sharma, 2013). However, several compartments that become important in semi-arid ecosystems (like multi-stemmed trees and shrubs, succulents, and soils with high carbonate content) require an adaptation of these standard procedures. The most important challenges that has to be considered for a complete and effective C pools quantification of these forest includes: (i) an adaptation of the globally standardized methods to effectively quantify plant biomass from different species showing different allometric relationships; (ii) deep soil sampling to include most of the SOC distribution across soil profiles of these systems; and (iii) quantification of SIC which could be an important and dynamic component of the total C of semi-arid systems. The research presented in this paper aimed to quantify in detail the aboveground and soil C pools of ecosystems under different land-uses in the semi-arid Chaco of Argentina, including trees, shrubs, non-woody vegetation, fine and coarse woody debris, and superficial and deep soil organic and inorganic C.

2. Materials and methods

2.1. Study area and experimental design

The study was carried out in the southern extreme of the Gran Chaco, in Córdoba Province, Argentina (c. 31°17'–31°50'S and 65°16'–65°32'W). The climate is subtropical with a mean annual precipitation of 600 mm distributed in spring–summer (October–March) and a mean annual temperature of 18 °C. Soils are mainly sandy-loam aridisols of alluvial origin (Gorgas and Tassile, 2003). The dominant vegetation is a xerophytic forest with *Aspidosperma quebracho-blanco* and *Prosopis flexuosa* as canopy and subcanopy dominants, respectively. The shrub layer is often dense and dominated by *Mimozyanthus carinatus*, *Acacia gilliesii*, and *Larrea divaricata* (Cabido et al., 1992).

During the December 2007–February 2008 summer, we sampled five different ecosystem types in the area, originally developed from the same vegetation, under the same climate and on highly similar substrate and topography. The selected ecosystem types corresponded to the most common combinations and intensities of livestock grazing and logging over the original Chaco forest. Sampled ecosystem types were: Primary forest, with no significant logging or livestock grazing in the past seven and five decades, respectively; Secondary forest, which has currently light selective logging and low cattle and goat stocking rates; Closed species-rich shrubland, with a high shrub species diversity and under current moderate to heavy logging and moderate-high cattle and goat stocking rate; Open shrubland strongly dominated by *L. divaricata*, with heavy logging and high cattle and goat stocking rate during the past decades, now decreasing due to declining productivity; and irrigated crop (potato) traditionally cultivated in the area using a gravitational irrigation system. Potato production systems typically include two potato crops per year (in summer and winter) and an average water requirement for the area of 500 mm per crop (Tapella, 2012). We identified four plots (replicates) of each ecosystem type at a distance of at least 1 km from each other, except in the case of the potato culture, where the plots were closer. Each sampling plot had 50 m × 50 m and was as homogeneous as possible in terms of vegetation, soil, and topography. At each site we sampled basic soil parameters including total N (%), pH and texture to confirm similarities among plots. All these procedures were carried out following Sparks (1996).

2.2. C Pools quantification

In order to estimate the vegetation C pools, at each 50 m × 50 m plot, we quantified biomass in trees, shrubs, non-woody vegetation, fallen leaf, and fine woody material (fine debris), as well as coarse fallen woody material and standing dead trees (coarse woody debris). The sum of C in trees, shrubs, and non-woody vegetation represented the C pool in the aboveground plant standing biomass compartment (ASB). The sum of C in fine debris and that in coarse woody debris (CWD) represented the C pool in the aboveground plant dead biomass compartment (ADB).

In order to estimate soil C pools, we took a compound soil sample (3 cores) at each plot and at four depths (0–10, 10–30, 30–100, and 100–200 cm) with a soil corer of 10 cm diameter. From each soil sample, we determined soil organic and inorganic C (SOC and SIC, respectively). We expressed all plant and soil C pools in Mg C ha⁻¹.

2.2.1. Aboveground plant standing biomass (ASB)

We surveyed all trees greater than 5 cm diameter at breast height in each plot and estimated their dry biomass (ASB, kg) by the allometric model proposed by Chave et al. (2014) using

diameter at breast height (DBH, cm), height (H , m) and wood specific gravity (WSG, g cm^{-3}) as predictor variables:

$$\text{ASB} = 0.0673 \times (\text{WSG} \times \text{DBH}^2 \times H)^{0.976} \quad (1)$$

We recorded DBH and H of each individual tree, and measured WSG at the species level following the methodology of Pérez-Harguindeguy et al. (2013). We surveyed a total of 926 tree individuals across all plots. To test the local applicability of Eq. (1), we correlated the estimations of individual tree biomass obtained with Eq. (1) with those obtained using local species-specific equations when available (Gaillard de Benitez et al., 2002a,b,b; Iglesias and Barchuk, 2010). The correlation was very strong ($R^2 = 0.96$, $P > 0.0001$, $N = 660$, see Fig. A1 and Table A1 for details), we therefore applied Eq. (1) to estimate the individual biomass of all tree species sampled within the allometric variables range considered by the equation (DBH = 5–212 cm; $H = 1.20$ –70.7 m and $\text{WSG} = 0.09$ –1.20 g cm^{-3}) (Chave et al., 2014).

All shrubs (i.e., multi-stemmed woody plants) and small trees (those with a single main stem with DBH < 5 cm) were sampled in three 5 m × 5 m subplots randomly distributed within each 50 m × 50 m plot. Their individual biomass was estimated using locally developed species-specific equations (Conti et al., 2013; Hierro et al., 2000; Iglesias and Barchuk, 2010). In the case of species for which there was no published equation, we used local multispecies aboveground biomass regression models to estimate the individual biomass according to Conti et al. (2013). We measured a total of 790 shrubs and small trees individuals across all plots. Then all individual biomass measurements were aggregated across each plot (for trees) or subplot (for shrubs) in order to obtain the total tree and shrub biomass per hectare. The C content of the woody biomass was considered as 50% of the dry biomass (Brown, 1997). All detailed equations used for shrub individual biomass estimations are presented in Table A2.

In order to quantify the uncertainty of biomass C estimates generated by the use of biomass models, we propagated the associated error following a Monte Carlo approach (Chave et al., 2004). We included potential imprecisions of sampling allometric variables (height, diameter, crown diameter, wood density, and C content) that were used as input for the biomass models. We also included the uncertainty associated to the chosen allometric model. To do this, we expanded the model function using a higher order Taylor series, which correct for biases in nonlinear expressions (Spiess, 2014). Since we applied the models within their range of applicability (i.e., all individual trees were within the range of applicability of Chave et al.'s model and all the shrub's model has been constructed locally considering the range of the inputs variables), we did not include this potential error on the uncertainty estimate. At each iteration (we run a total of 1000 iterations) we estimated a random value for each allometric variable and for the estimated individual C content by sampling from their distributions, based on the mean and standard error of each variable (Yanai et al., 2010). Additionally, we used the same procedure to obtain and incorporate the error associated to plot variability (intra-plot variability for shrubs as well as inter-plot variability for shrubs and trees).

We quantified non-woody vegetation (including forbs, grasses, and succulents) by harvesting all standing non-woody aboveground biomass over the soil in six subplots (0.5 m × 0.5 m) randomly distributed within each 50 m × 50 m plot during the peak of the growing season. A subsample of the material collected at each subplot was oven-dried at 80 °C for 3 days, weighed, ground and kept in a muffle furnace (INDEF mod. 331) at 500 °C for 4 h to obtain the C content of the subsample following a loss-in-ignition approach (Schlesinger and Hasey, 1981). This value was used to convert total dry biomass in each subplot to C.

2.2.2. Aboveground plant dead biomass (ADB)

The accumulated fine debris was sampled by a single collection of all plant fallen material accumulated on the ground surface in six subplots (0.5 m × 0.5 m) randomly distributed within each 50 m × 50 m plot. The sampling was carried out in autumn, after most of the senescent parts of deciduous and semi-deciduous species material had fallen.

Woody debris >5 cm diameter and standing dead trees (CWD) were sampled in three 5 m × 5 m subplots randomly distributed within each plot. Coarse fallen woody debris was directly weighted in the field at each subplot. Standing dead tree biomass was obtained using cylindrical volume models including diameters and height, and multiplying the volume by the species WSG to obtain the dry biomass. To estimate the uncertainty of quantify standing coarse fallen woody debris by the use of models, we used the procedure described before for shrubs and trees (Section 2.2.1), including the error in field measured allometric variables from dead stumps (diameter, height, wood density, and C content). The C content of debris was estimated following the same procedure described previously to obtain the C content of non-woody vegetation (a loss-in-ignition approach).

2.2.3. Soil C pools

We air-dried all soil samples and sieved them through a 2-mm mesh before performing chemical analyses. We determined organic C (g kg^{-1}) using an oxidation in acid medium procedure ('Walkley & Black'; Nelson and Sommers, 1996). We chose this analytical procedure because it allowed measuring only the organic fraction of the soil sample and thus distinguishing it from the inorganic fraction. We calculated soil bulk density (BD) by measuring the mass of dry soil contained in a metal cylinder which measured 4.5 cm in diameter and 10 cm in height. The samples were oven-dried at 105 °C for 48 h to obtain the dry mass of the soil. No adjustment for rocks or coarse fragments was necessary because soil samples did not contain any. Below 30 cm of soil depth, BD was estimated using the equation proposed by Post and Kwon (2000); due to the logistical constraints to obtain an intact soil sample without losing sampling precision.

SIC across the soil profile was quantified as carbonate content for each depth interval. We heated a weighed amount of sample with HCl with a back-titration of the remaining acid with NaOH (Sparks, 1996). Calcium carbonate equivalents were converted to C content by multiplying them by 0.12, the mole fraction of C in CaCO_3 .

SOC and SIC at each depth interval was corrected to an equivalent soil mass using the approach presented by Ellert and Bettany (1995) considering as the reference soil mass for each layer the average of soil under primary forest.

For the purpose of this work, we calculated total ecosystem C (TEC) as the sum of all C pools measured: ASB, ADB, SOC, and SIC. Total organic C (TOC) only included ASB, ADB, and SOC. This distinction was made because, while a reduction in total organic C in this system represents a net release of CO_2 to the atmosphere, a reduction in the inorganic compartment deserves a more complex analysis, particularly of the fate of the leached carbonate (e.g., to the groundwater, some of which is used in irrigation; Sanderman, 2012).

To calculate the uncertainty included in the estimations of TEC, at each Monte Carlo iteration, we added up the randomly sampled values for each of the estimated and quantified C stocks (obtained as described above in Section 2.2.1) to obtain an expected mean and associated error of TEC. Uncertainty estimation and propagation by Monte Carlo was quantified using the package "propagate" (Spiess, 2014) under R statistical software (R Development Core Team, 2011).

2.3. Statistical analysis

Differences in C pools across ecosystem types were tested by one-way ANOVA following linear models when data had normal distribution and homogeneous variance. Normal distribution was tested using Shapiro–Wilks analysis and homogeneous variance was analyzed according to Levene's test. When data did not present normal distribution, a log transformation was applied, and when presented heterogeneous variance we used linear mixed models, and evaluated fit using the akaike information criterion (Burnham and Anderson, 2002). Multiple comparisons were performed using Fisher's LSD post hoc test with $\alpha = 0.05$. Ecosystem types with total absence of a specific C pool (e.g., C stored in trees was absent in cultivated sites) were not included in the mean comparison analysis but were included in graphs for reference. Statistical analyses were performed using Infostat v. 2011 Statistical Package (Di Rienzo et al., 2011).

3. Results

Plant and soil C pools differed significantly between ecosystem types where basic soil parameters were not statistically different (Table 1).

When all aboveground standing biomass (ASB) components (trees, shrubs, and non-woody vegetation) were considered together, primary and secondary forest showed the largest C pool; closed species-rich shrublands and open *Larrea* shrublands had intermediate values while potato crop sites showed the lowest value (Table 2 and Fig. 1(a)). Trees and shrubs represented the most important proportion of the C stored in the aboveground standing biomass with their relative proportions varying according to the ecosystem type considered. As expected, C in trees was highest in primary and secondary forest (64.3% and 71% of ASB, respectively), while C in shrubs was the main standing biomass compartment in closed species-rich and open *Larrea* shrublands (64.5% and 51% of

ASB, respectively) (Table 2). The uncertainty due to the application of biomass models is higher for shrubs than trees, but in any case represented more than the 7% of the mean for the former, and lower than 2% of the mean for the latter. In absolute terms, the biases did not represent more than 1 Mg C ha⁻¹ in any case (Table A3).

Aboveground dead biomass (ADB), including fine and coarse debris, differed significantly across the ecosystem types considered with primary and secondary forest having the highest values of debris (Table 2 and Fig. 1(b)). C stored in fine debris (leaf litter and fine woody debris), was highest in primary forest, intermediate in secondary forest, and lowest in closed species-rich and open *Larrea* shrublands (Table 2). In all ecosystem types except the potato crop sites (where no debris remained), C stored in fine debris represented more than 50% of the total aboveground dead biomass.

When SOC was considered across the entire soil profile (0–200 cm), organic C pools did not differ significantly between sites (Table 2 and Fig. 1(c)). However, significant differences became apparent when SOC pools were analyzed by soil depth (Table 2). Surface (0–10 cm) and subsurface (10–30 cm) SOC pools were highest in primary and secondary forest. Deeper SOC pools (below 30 cm depth) were not significantly different among ecosystem types. SOC pools at 30–100 cm represented the highest proportion in all ecosystem types (more than 35% of total SOC), excepting in *Larrea* shrublands where the deepest layer represented the largest proportion.

Total SIC content (0–200 cm) showed significant differences across ecosystem types (Table 2 and Fig. 1(d)). Soils under potato cultivation had the lowest SIC content across the considered ecosystem types. In contrast, primary forest has the highest amount of SIC. Differences in total SIC content across ecosystem types were in fact caused by a reduction in SIC content in the deepest layers (>30 cm depth). Above 30 cm depth there was no difference in SIC between ecosystem types (Table 2).

Table 1
Basic soil properties under different ecosystem types (mean values with standard error).

Soil properties	Ecosystem types					Statistical descriptors	
	Primary forest	Secondary forest	Closed species-rich shrubland	Open <i>Larrea</i> shrubland	Potato crop	P	F
Soil layer 0–10 cm							
Bulk density (g cm ⁻³)	1.22 ± 0.03a	1.43 ± 0.02b	1.46 ± 0.04b	1.50 ± 0.06b	1.48 ± 0.07b	0.0036	6.25
OC (g kg ⁻¹)	16.30 ± 0.77a	15.98 ± 1.42a	9.73 ± 1.47b	6.65 ± 0.26b	7.95 ± 1.56b	0.0001	14.12
Nt (g kg ⁻¹)	1.69 ± 0.09a	1.47 ± 0.33ab	1.26 ± 0.17abc	0.82 ± 0.08c	0.95 ± 0.17bc	0.0312	3.56
pH	6.9 ± 0.1a	6.7 ± 0.4a	7.1 ± 0.2a	7.0 ± 0.2a	6.8 ± 0.3a	0.6532	0.62
Clay (%)	12.35 ± 0.41a	12.20 ± 0.36a	12.65 ± 0.59a	9.78 ± 0.66a	11.38 ± 1.42a	0.1230	2.16
Soil layer 10–20 cm							
Bulk density (g cm ⁻³)	1.30 ± 0.03a	1.41 ± 0.02a	1.40 ± 0.04a	1.40 ± 0.04a	1.62 ± 0.07b	0.0014	7.73
OC (g kg ⁻¹)	8.55 ± 0.62a	8.31 ± 0.68a	6.42 ± 0.22ab	5.10 ± 0.48b	7.25 ± 1.36ab	0.0371	3.37
Nt (g kg ⁻¹)	1.05 ± 0.07a	0.83 ± 0.10a	0.88 ± 0.02a	0.72 ± 0.05a	0.91 ± 0.15a	0.1826	1.79
pH	7.8 ± 0.1a	7.7 ± 0.03a	7.7 ± 0.1a	7.8 ± 0.3a	7.3 ± 0.1a	0.1068	2.30
Clay (%)	8.20 ± 0.60a	11.20 ± 0.78a	10.95 ± 0.62a	8.88 ± 1.03a	9.70 ± 1.22a	0.1247	2.15
Soil layer 30–100 cm							
Bulk density (g cm ⁻³)	1.60 ± 0.01a	1.59 ± 0.004a	1.58 ± 0.01a	1.60 ± 0.01a	1.59 ± 0.01a	0.7057	0.54
OC (g kg ⁻¹)	2.79 ± 0.52a	3.40 ± 0.23a	3.76 ± 0.64a	2.72 ± 0.83a	3.29 ± 0.56a	0.6986	0.55
Nt (g kg ⁻¹)	0.53 ± 0.02a	0.65 ± 0.13a	0.56 ± 0.03a	0.49 ± 0.05a	0.47 ± 0.07a	0.4961	0.89
pH	7.1 ± 0.1a	7.2 ± 0.3a	7.5 ± 0.2a	7.4 ± 0.1a	6.7 ± 0.3a	0.4362	1.00
Clay (%)	7.70 ± 0.18a	9.13 ± 0.74a	8.00 ± 0.68a	7.15 ± 0.84a	8.38 ± 1.40a	0.5805	0.74
Soil layer 100–200 cm							
Bulk density (g cm ⁻³)	1.63 ± 0.002a	1.62 ± 0.003a	1.62 ± 0.01a	1.61 ± 0.01a	1.63 ± 0.003a	0.3849	1.12
OC (g kg ⁻¹)	0.85 ± 0.12a	1.09 ± 0.21a	1.24 ± 0.42a	2.10 ± 0.94a	0.86 ± 0.20a	0.3793	1.13
Nt (g kg ⁻¹)	0.23 ± 0.01a	0.28 ± 0.02a	0.30 ± 0.03a	0.74 ± 0.54a	0.20 ± 0.03a	0.3496	1.21
pH	7.4 ± 0.2a	7.6 ± 0.1a	7.8 ± 0.1a	7.7 ± 0.2a	7.5 ± 0.2a	0.1754	1.83
Clay (%)	6.50 ± 0.37a	7.13 ± 0.28a	6.25 ± 0.33a	5.93 ± 0.51a	5.88 ± 0.24a	0.1465	2.00

Different letters indicate significant differences between the same compartment across different ecosystem types (Test Fisher's LSD, $P < 0.05$).

Table 2Carbon pools (Mg ha⁻¹) of different plant and soil compartments in different ecosystem types (mean values with standard error).

C pools	Ecosystems types					Statistical descriptors	
	Primary forest	Secondary forest	Closed species-rich shrubland	Open <i>Larrea</i> shrubland	Potato crop	P	F
C in non-woody vegetation	0.47 ± 0.07b	0.26 ± 0.08b	0.82 ± 0.39b	1.45 ± 0.07a	0.44 ± 0.05b	0.0051	5.96
C in shrubs	11.83 ± 0.5a	7.42 ± 1.15bc	9.84 ± 2.01ab	4.91 ± 1.37c	0	0.0202	4.80
C in trees	22.13 ± 2.26a	18.75 ± 4.07a	4.61 ± 1.27b	3.25 ± 1.16b	0	0.0002	15.11
C in fine debris	6.19 ± 0.61a	3.98 ± 0.21b	1.91 ± 0.53c	0.92 ± 0.30c	0	<0.0001	27.54
C in coarse woody debris	2.63 ± 1.02a	3.70 ± 2.46a	0.71 ± 0.47a	0.63 ± 0.59a	0	ns	1.18
SOC _{0–10 cm}	19.80 ± 0.75a	19.46 ± 1.73a	11.84 ± 1.79b	8.10 ± 0.32b	9.68 ± 1.90b	<0.0001	14.50
SOC _{10–30 cm}	22.22 ± 1.66a	23.20 ± 1.87a	17.59 ± 0.42ab	13.74 ± 1.09b	19.05 ± 3.59ab	0.0327	3.51
SOC _{30–100 cm}	31.05 ± 5.69a	40.06 ± 2.40a	43.24 ± 6.68a	31.63 ± 8.75a	39.95 ± 6.44a	ns	0.75
SOC _{100–200 cm}	13.82 ± 1.97a	18.48 ± 3.30a	20.99 ± 6.60a	34.70 ± 15.61a	15.78 ± 3.03a	ns	1.09
SIC _{0–10 cm}	2.39 ± 0.49a	2.74 ± 0.44a	1.92 ± 0.17a	2.01 ± 0.24a	1.92 ± 0.27a	ns	1.10
SIC _{10–30 cm}	4.50 ± 0.28a	4.93 ± 0.44a	4.98 ± 0.49a	5.01 ± 0.66a	4.11 ± 0.66a	ns	0.55
SIC _{30–100 cm}	53.81 ± 10.49a	41.12 ± 3.90ab	43.54 ± 3.37a	40.90 ± 2.67ab	27.84 ± 1.60b	0.053	3.11
SIC _{100–200 cm}	115.90 ± 16.88a	86.03 ± 1.24a	85.02 ± 6.58a	94.68 ± 18.09a	36.27 ± 6.20b	0.0061	5.93
C in aboveground plant standing biomass (ASB)	34.43 ± 2.04a	26.43 ± 4.93a	15.27 ± 2.53b	9.61 ± 2.53bc	0.44 ± 0.05c	<0.0001	18.36
C in aboveground plant dead biomass (ADB)	8.83 ± 1.45a	7.68 ± 2.61a	2.62 ± 0.98b	1.55 ± 0.75b	0	0.0176	5.01
SOC _{0–200 cm}	86.89 ± 5.04a	101.19 ± 7.88a	93.65 ± 12.32a	88.17 ± 24.41a	84.45 ± 14.75a	ns	0.21
SIC _{0–200 cm}	190.77 ± 17.14a	134.82 ± 4.80b	135.45 ± 8.87b	144.19 ± 21.71b	69.60 ± 7.67c	0.0006	10.91
Total organic ecosystem C (TOC)	130.14 ± 5.19a	135.30 ± 3.93a	111.54 ± 9.45a	99.33 ± 22.98a	83.16 ± 20.75a	ns	2.20
Total organic ecosystem C ₃₀ ^a (TOC ₃₀)	85.27 ± 3.37a	76.76 ± 3.94a	47.32 ± 4.20b	32.99 ± 1.66c	33.80 ± 0.05c	<0.0001	37.54
Total ecosystem C (TEC)	322.68 ± 10.24a	270.11 ± 5.66b	246.99 ± 17.35b	259.9 ± 16.07b	152.76 ± 28.30c	0.0003	12.54

Different letters indicate significant differences between the same compartment across different ecosystem types (Test Fisher's LSD, $P \leq 0.05$, $n = 4$ in all compartments except for C in non-woody vegetation in potato crops, and SIC in primary forest, open *Larrea* shrubland and potato crops, where $n = 3$). SOC: soil organic carbon, SIC: soil inorganic carbon, P: statistical significance, F: Fisher's statistic, ns: no statistical significance ($P > 0.05$).

^a Calculated including all aboveground compartments and SOC only at 0–30 cm depth.

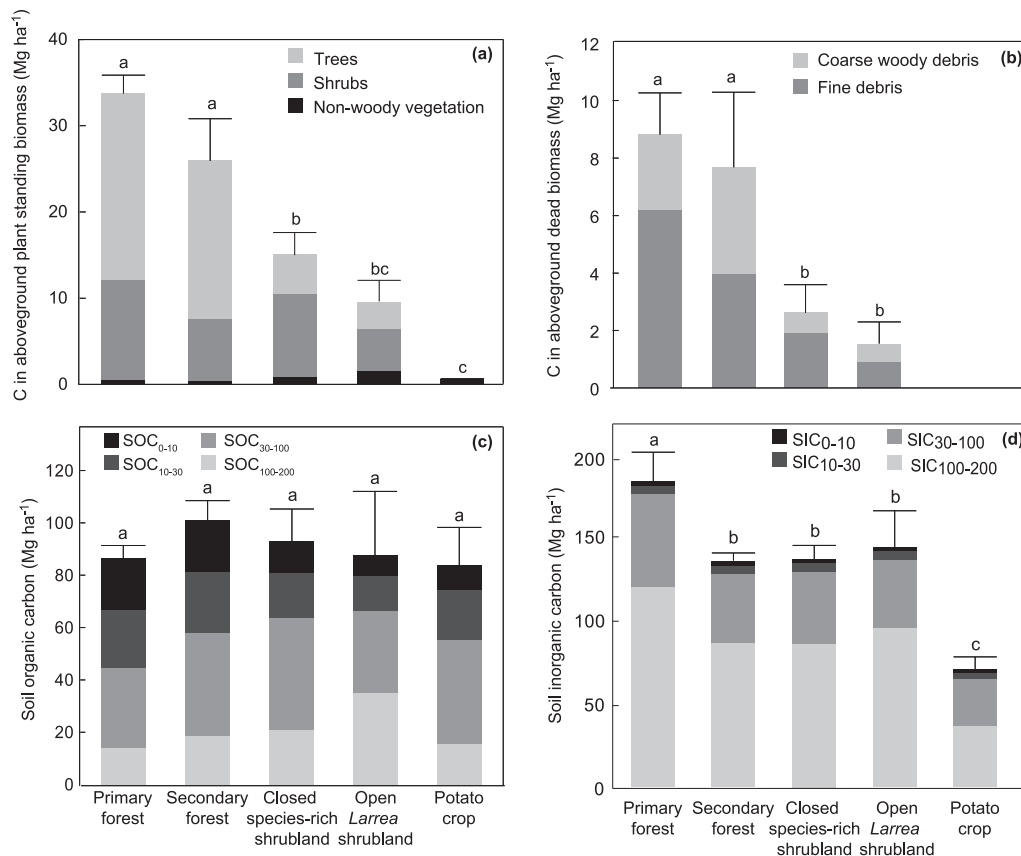


Fig. 1. Plant and soil C pools in different ecosystems types of the semi-arid Chaco of central Argentina. (a) C in aboveground plant standing biomass and distribution over its components; (b) C in aboveground dead biomass and distribution over its components; (c) soil organic carbon (SOC) and its distribution along the soil profile; (d) soil inorganic carbon (SIC) and its distribution along the soil profile. Different letters indicate significant differences across ecosystem types (Test Fisher's LSD, $P < 0.05$). Error bars indicate standard errors.

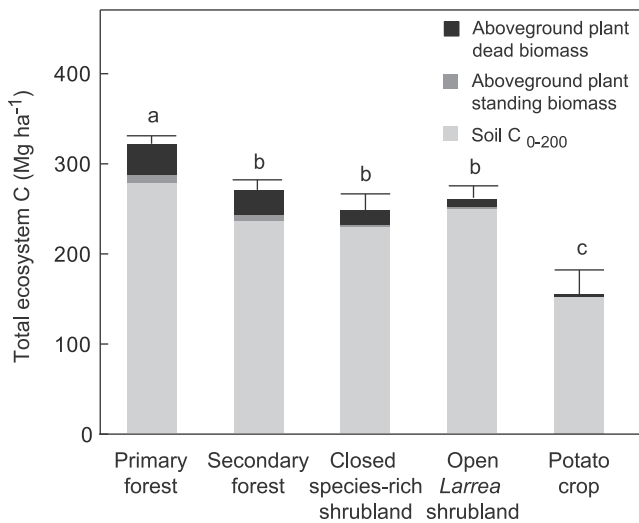


Fig. 2. Total ecosystem C in different ecosystem types of the semi-arid Chaco forest of central Argentina. Different letters indicate significant differences across ecosystem types (Test Fisher's LSD, $P < 0.05$). Error bars indicate standard errors. Different colors within the bars represent different C pool compartments within the ecosystem. Soil C for each layer includes organic and inorganic C.

Total ecosystems C pools including only the organic component (TOC) did not differ significantly across ecosystem types (Table 2). However, when TOC was considered including only the first 30 cm soil depth, TOC showed statistical differences across sites, where primary and secondary forests had the highest C pool, closed species-rich shrublands intermediate C pool, and open *Larrea* shrublands and potato crops the lowest (Table 2).

Total ecosystem C pools (TEC) differed significantly between ecosystem types (Table 2 and Fig. 2), with the highest C storage in primary forest, intermediate in secondary forests, closed shrublands and open *Larrea* shrublands, and lowest in potato crop sites. The uncertainty analysis on the TEC estimation showed that open *Larrea* shrublands had the highest associated error. The expected mean had a bias of $17.95 \text{ Mg C ha}^{-1}$ (7%) compared with the sampled mean, while for the other ecosystem types, the bias was significantly lower (c. 1.1 Mg C ha^{-1} for primary, secondary forests and closed species shrublands, and c. 3.2 Mg C ha^{-1} for potato crops). The mean, confidence intervals and bias resulting from the uncertainty analysis are shown in Table A3.

4. Discussion

In what is, to our knowledge, the first empirical quantification of total ecosystem C pools for semi-arid Chaco forest ecosystems, we found that the magnitude of different C pools and their contribution to total ecosystem C storage are deeply affected by the land-use transitions that are occurring widely over the region.

Previous estimates of semi-arid Chaco forests C storage considering only aboveground compartments and upper soil profiles found values in the range of those reported here for the same compartments; an average of 55 Mg C ha^{-1} in woody biomass from semi-arid Chaco forests of northern Argentina in Gasparri and Baldi (2013); $34.4 \text{ Mg C ha}^{-1}$ in aboveground pools plus $50.4 \text{ Mg C ha}^{-1}$ in 30 cm organic soil depth in Manrique et al. (2011); $30.4 \text{ Mg C ha}^{-1}$ in woody biomass and $34.6 \text{ Mg C ha}^{-1}$ in 20 cm soil depth in Bonino (2006); $69.9 \text{ Mg C ha}^{-1}$ in 20 cm organic soil depth in Abril and Bucher (2001). Other works including aboveground compartments and also deeper organic soils profiles (up to 1 m depth) based on indirect estimates (as function of aboveground biomass and 0.2 m soil C) resulted in $99.7 \text{ Mg C ha}^{-1}$ of total organic C (Gasparri et al., 2008), similar to the ones measured directly in

our study. Our work updates and adds more detail to previous estimations of aboveground standing biomass, empirically quantifying shrubs, non-woody vegetation and coarse woody debris, and adding new results on the C storage in the deepest soil layers as well as a complete profile for SIC, not only for forest under different managements but also for shrublands and crops. We also include the quantification of uncertainty related to the use of biomass models and the field sampling of allometric variables, which has not been performed previously for results obtained in the study area.

One important finding of this work was the magnitude of the C pool represented by shrubs (at least 28% of the aboveground standing biomass in all ecosystems except cultivated ones), usually underestimated in C forest assessments. Because to date there is no locally developed equations or direct estimation of belowground biomass, we have not included estimation of root C stocks. However, a rough estimate based on Cairns et al. (1997) suggests that this compartment may represent at least 25% of the total C in biomass across all sites. It is thus urgent to develop specific estimations of the C contained in the roots of these semi-arid systems. As expected, C stored in aboveground plant dead biomass decreases under forest management since all land-use practices (logging and grazing) directly remove plant material from the system. It is important to note that CWD represents the C pool with the highest uncertainty. This variation is related to the probability to find a standing dead tree in any plot which will contribute disproportionately to stand-level CWD.

All these aboveground changes had important implications for the dynamics of soil organic carbon stocks under different ecosystem types. In this respect, we found a considerable effect of land use change on SOC in the 0–30 cm depth in this semi-arid Chaco forests, reinforcing previous findings in different ecosystems worldwide (Don et al., 2011; Guo and Gifford, 2002; Lal, 2005; Murty et al., 2002; Wiesmeier et al., 2012; Zinn et al., 2005). However, the percentage of reduction found in this work for the forest to crop transition (31.6%) is greater than the upper limit of relative C loss presented in those studies, such as the 25% of C loss in tropical soils (Don et al., 2011) and 22.1% loss found in a meta-analysis of predominantly tropical sites (Murty et al., 2002). The C reduction of the SOC stored at 0–30 cm between semi-arid Chaco forest and crop transition represented an absolute loss of SOC of $13.3 \text{ Mg C ha}^{-1}$. This value is lower than the C losses reported for tropical ($20.1 \text{ Mg C ha}^{-1}$; Don et al., 2011), temperate (33 Mg C ha^{-1} ; Davidson and Ackerman, 1993) and boreal ecosystems (83 Mg C ha^{-1} ; Grünzweig et al., 2004) after forest to crop transition, but is far from negligible and represents a very important loss of soil fertility in these low-productivity semi-arid ecosystems (Lal, 2004). The conversion of primary and secondary forest to open *Larrea* shrubland – normally the result of long-term heavy logging and overgrazing – also resulted in a loss of soil organic C (0–30 cm) similar (and even higher in absolute terms) than forest replacement by crops ($20.18 \text{ Mg C ha}^{-1}$ or 48%). It is important to note that, although not statistically significant, the open *Larrea* shrubland showed slightly lower clay content for the upper soil increments, compared to other ecosystems. This slightly low clay content could be possibly related with the processes of soil erosion that characterize this ecosystem type. Since SOC stabilization is heavily controlled by the soil clay content (Jobbagy and Jackson, 2000), it could be overestimating the differences in superficial SOC in relation to the other ecosystem types considered. Open *Larrea* shrubland also showed the highest uncertainty in estimations, which could be related to both, an increased cover and soil heterogeneity compared with the other ecosystem types and the highest proportion of shrubs with a larger associated biomass model error compared to tree biomass models. These results highlight the need for an increased effort in sampling more

heterogeneous sites and in the construction and calibration of local shrub biomass models.

In agreement with previous works (Guo and Gifford, 2002), we found that SOC below 30 cm (30–200 cm soil depth) was not affected by land-use. When considering the complete soil profile up to 200 cm there were no net changes in the absolute magnitude of SOC pools among ecosystem types. However, since the larger proportion of SOC is stored below 30 cm depth, any change in land-use potentially leading to redistribution of fresh C along the soil profile (e.g., vertical C redistribution related with forest conversion to crops) could stimulate the loss of a large amount of deep carbon in these systems (Chaopricha and Marín-Spiotta, 2014; Fontaine et al., 2007; Rumpel and Kögel-Knabner, 2011).

Below 100 cm depth, SIC overtakes SOC as the most important form of C, where it was, on average, four times more abundant as SOC in the ecosystem types considered. An increase of SIC content with depth is a pattern commonly found in arid and semi-arid ecosystems globally. SIC amounts in Chaco forest ($\sim 48 \text{ Mg C ha}^{-1}$ up to 1 m depth on average) are within the range to those found in Mongolian steppes (e.g., 44 Mg C ha^{-1} ; Zhi-Ping et al., 2013) and in arid and semi-arid regions of China ($42.9 \text{ Mg C ha}^{-1}$; Mi et al., 2008). Although this soil inorganic pool is commonly considered a relatively stable compartment, our findings indicate that land-use conversion significantly reduced the calcium carbonate content of soils, mainly in the 30–200 cm soil layer. Recent works had reported that disturbance profoundly affect the soil water dynamics across the soil profile, where a reduced soil water consumption after biomass removal increase the soil moisture levels (Jayawickreme et al., 2011; Santoni et al., 2010), potentially increasing carbonate leaching and dissolution processes within the soil. The effect of irrigation practices could increase even more the carbonate leaching in the sampled soil layers under potato crops (Wu et al., 2009). It is important to note that although most crop management in the study area requires irrigation, this is not always the case in other, more humid sections of the Chaco, so this pattern may not be common across the whole great Chaco region.

Unlike SOC pools, a decrease in SIC content does not necessarily represents a net loss of CO_2 from the ecosystem, mainly depending on the source and fate of carbonic acid (HCO_3^-). If the HCO_3^- derives from root respiration and decomposition and is simply re-precipitated deeper in the soil profile, then the process is C neutral. If the HCO_3^- instead is leached from the soil and enters a longer-lived C pool (e.g., groundwater), then the process of carbonate dissolution will be a net C gain. If the HCO_3^- is leached back from a long-term reservoir in the groundwater into a surface water system (e.g., pivot irrigation systems), then it will result in a net source of C to the atmosphere (Sanderman, 2012). The same author also found that the combined effect of nitrate leaching and the application of ammonium-based fertilizers could result in a soil acidification that could accelerate the process of carbonate dissolution in cultivated lands. The potential effect of management over the C sequestration in long term reservoirs like calcium carbonate and carbonic acid in groundwater undoubtedly deserves further analysis.

Total ecosystems carbon stocks (TEC) were reduced under more intense land-uses, indicating that all considered management intervention over natural forests reduces the C stored of these ecosystems. However, when considering total organic C stocks on the first 30 cm of soil depth where most biological activity occurs, we found that forest with some wood extraction and low levels of livestock grazing (secondary forest) had still high C pools (aboveground and soil up to 30 cm depth) also providing other important ecosystem benefits to people, such as fuel, construction materials, and food to subsistence and other types of farmers (Tapella, 2012). Although closed species-rich shrublands had smaller C pools than forested ecosystem types, the reduction in

C was lower than that of open *Larrea* shrublands and croplands, specifically when considering TOC up to 30 cm depth. The former also provides several additional provisioning and cultural ecosystem services linked mainly to the livelihood of subsistence farmers (Silvetti, 2012; Tapella 2012).

5. Conclusions

Our results, based on detailed empirical measurements of several C pools in ecosystems under different present and historical land-use regimes in the semi-arid Chaco forest, indicate that forest management, and particularly forest conversion to crops, is associated with reductions of C in aboveground standing biomass and also with decreases in organic C in the upper soil layers due to reduced input from plant debris. Land-use not only alters the amount of C stored in plant biomass and in the organic fractions of the soil (SOC) but also in the inorganic C fraction. The latter is an important but often neglected component of C pools in semi-arid systems.

At present, Chaco forests are quickly being replaced by intensively managed systems, particularly large-scale agriculture (Hansen et al., 2013; Hoyos et al., 2013; Zak et al., 2004). Rather than slowing down, this trend is likely to continue or even accelerate (Cáceres, 2014; Gasparri and Grau, 2009; PEAA, 2010). If so, then a severe reduction in C pools in the semi-arid Chaco forest is likely. This would add to the broader set of losses of ecosystem services associated with these land-use trajectories at local, regional, and global scales (Tapella, 2012).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2014.07.025>.

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